TWO LITTLE-KNOWN SPECIES OF ELEUTHERODACTYLUS (AMPHIBIA: LEPTODACTYLIDAE) FROM THE SIERRA DE LA MACARENA, COLOMBIA

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Abstract.—Two sympatric species of Eleutherodactylus occur in the cloud forest of La Macarena, Colombia. One is an undescribed species, herein named Eleutherodactylus savagei. This species resembles E. fenestratus, from which it differs in skin texture, in having a heel tubercle, and in throat pattern.

The other Macarena species is *Eleutherodactylus frater*. The species *E. savagei* and *E. frater* are morphologically similar and have similar breeding calls, but appear to be reproductively isolated from each other by differences in habitat, period of activity, and possibly by subtle differences in call.

A field party from the University of Texas at Arlington collected specimens and obtained voice recordings of two species of *Eleutherodactylus* in the cloud forest of the Macarena Mountains, Departamento del Meta, Colombia, in March 1971. The calls were recorded with a Uher 4000 Report L tape recorder and sound spectrograms were made from the tapes in the laboratory with a Kay Elemetrics Corporation "Sona-Graph."

One of the species is *Eleutherodactylus frater*, a small arboreal form whose relationships have been in doubt. The other species is unnamed. For it, we propose the name:

Eleutherodactylus savagei, new species (Figs. 1, 2)

Holotype.—UTA 3535, an adult male taken on the Sierra de la Macarena, ca. 35 km WSW Vistahermosa, Depto. Meta, Colombia, 1097-1128 m, on 20 March 1971 by W. F. Pyburn.

Paratypes.—UTA 3525-29, 3536-38, 5608-18; USNM 218054-62; AMNH 107557-65; CM 76154-62; KU 187001-09; all topotypes collected 17-20 March by W. F. Pyburn, J. R. Glidewell, and J. Taulman.

Diagnosis.—1) Skin of dorsum finely shagreened becoming more coarse posteriorly, that of venter smooth; no dorsolateral folds; 2) tympanum prominent, its length about 1/3 eye length; 3) snout subacuminate in dorsal view,

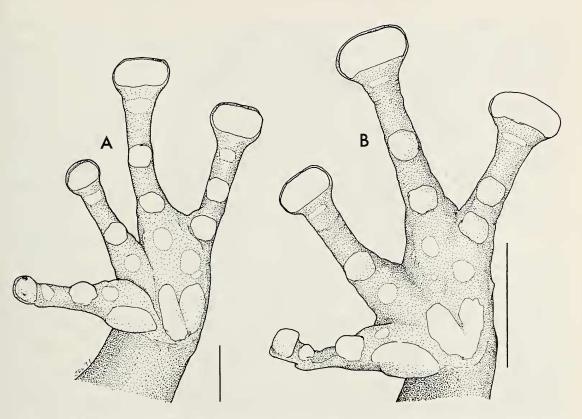


Fig. 1. Hands of (A) Eleutherodactylus savagei n. sp., UTA 5616, and (B) E. frater, UTA 3531. Lines equal 2 mm.

acutely rounded in lateral profile; snout long, E-N < eye length; 4) IOD broader than upper eyelid, flat; 5) vomerine odontophores triangular in outline; 6) males with vocal slits and white, non-spinous nuptial pads; 7) length of first and second fingers nearly equal; large pads on fingers III-IV; 8) fingers with slight lateral keels; 9) only antebranchial tubercle evident; 10) small tubercles on heel; no outer tarsal tubercles; inner edge of tarsus bearing ridge or series of tubercles; 11) two metatarsal tubercles, inner elongate, 4 times size of outer; supernumerary plantar tubercles at bases of toes; 12) toes bearing keels proximally; basally webbed (web not encroaching basal subarticular tubercles); 13) tan to brown with pattern vague except for black scapular spots and canthal-supratympanic stripe; throat peppered with brown, pigment extending onto chest as faint reticulation; groin and anterior and posterior surfaces of thighs uniform brown; shank bars oblique, narrower than interspaces; 14) adults moderate-sized, males 17.7–22.6 mm SVL ($\bar{x} = 20.2$, N = 7), females 31.0–34.7 mm ($\bar{x} = 32.6$, N = 17).

Most similar to E. fenestratus (Steindachner) but differing in skin texture (skin of dorsum finely shagreened vs with an interspersion of large warts), in having a small heel tubercle (none in E. fenestratus), and in having only faint marbling on the throat.

Description.—Head narrower than body, wider than long; HW in males



Fig. 2. Color pattern of Eleutherodactylus savagei n. sp., UTA 3527. Line equals 10 mm.

33.4–39.4 ($\bar{x}=37.2$, N = 5) percent SVL, in females 37.7–44.2 ($\bar{x}=40.2$, N = 18) percent; snout subacuminate in dorsal view, acutely rounded in lateral profile; snout long, E-N in males 73.5–75.8 ($\bar{x}=74.4$, N = 4) percent eye length, in females 79.5–95.0 ($\bar{x}=86.9$, N = 20) percent; nostrils weakly protuberant, directed laterally; canthus rostralis sharp, nearly straight (sinuous); loreal region flat (or very weakly concave), sloping abruptly to lip; some flaring of jaws posteriorly; interorbital region flat, no

cranial crests; upper eyelid width in males 83.0–100.0 ($\bar{x} = 89.9$, N = 4) percent IOD, in females 65.8–109.4 ($\bar{x} = 80.1$, N = 8) percent; supratympanic fold thick, obscuring upper and posterior edges of tympanum which is higher than long, length of tympanum in males 29.3–33.3 ($\bar{x} = 32.1$, N = 4) percent eye length, in females 27.5–35.7 ($\bar{x} = 32.3$, N = 20) percent; postrical tubercles not prominent; choanae round, moderately large, not concealed by palatal shelf of maxillary arch; vomerine odontophores slightly smaller than a choana, triangular in outline, separated on midline by a distance equal to odontophore width, median and posterior to choanae, each bearing 4–5 teeth; tongue slightly longer than wide, not notched posteriorly, posterior ½ not adherent to floor of mouth; males with vocal slits and a subgular vocal sac.

Skin of dorsum finely shagreened anteriorly, becoming more coarse posteriorly and very coarse with scattered tubercles on flanks; 1–2 small tubercles on upper eyelid; some evidence of a dorsolateral fold in scapular region but fading out in region of sacrum; large areolations below and posterolateral to vent, on posteroventral surfaces of thighs; no anal sheath or enlarged para-anal warts; skin of throat and venter smooth but with some suggestion of areolations encroaching from flanks; discoidal folds ill-defined; no ulnar tubercles except antebrachial; palmar tubercle bifid, much larger than oval thenar tubercle; supernumerary palmar tubercles relatively large (Fig. 1); subarticular tubercles subconical, round or slightly longer than wide; fingers bearing faint lateral keels; finger tips expanded forming pads (smallest on thumb), bearing broad discs on ventral surfaces; pads of III–IV largest (as large as tympanum) truncate, those of I–II round (Fig. 1); males bearing non-spinous nuptial pad; length of first and second fingers nearly equal.

One to two low round tubercles on heel, none on outer edge of tarsus; inner edge of tarsus bearing a long tubercle (sometimes one long and a short proximal one); inner metatarsal tubercle three times as long as wide; outer metatarsal tubercle round, $\frac{1}{4}$ size of inner; supernumerary plantar tubercles 4 (rarely 5), at bases of toes (some hint of others on rest of sole); basal toe webbing (not encompassing basal subarticular tubercles); lateral keels evident low on toes but indistinct distally; toes bearing pads and broad discs (smaller than those of outer fingers); heels of flexed hind legs overlap slightly; heel of adpressed hind leg reaches anterior edge of eye; shank of males 51.5-58.0 ($\bar{x}=54.5$, N=5) percent SVL, of females 50.0-58.0 ($\bar{x}=53.9$, N=20) percent.

Dorsum tan to brown with black scapular spots and nearly as dark canthal-supratympanic stripes; light brown sacral chevron, suprainguinal marks, interorbital bar, and flank bars (Fig. 2); anal triangle brown outlined with cream; 3–4 oblique bars on shank, less than to equal interspace width; a common variant has cream dorsolateral stripes along anterior ³/₅ body

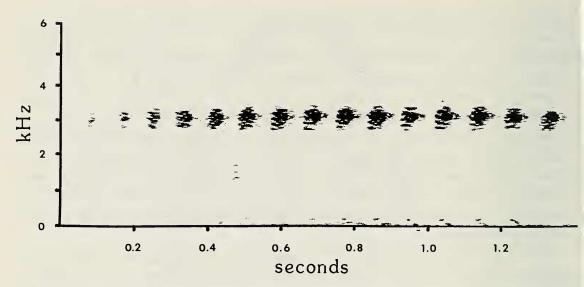


Fig. 3. Sound spectrogram of one complete call of *Eleutherodactylus savagei* (narrow band filter). Recorded 20 March 1971 at type locality (air temperature, 17.3°C).

(Fig. 2); throat lightly peppered with brown, sometimes extending onto chest as a reticulation; peppering on undersides of legs; groin and anterior and posterior surfaces of thighs uniform brown.

Measurements of holotype in mm.—SVL 21.2; shank 11.5; head width 7.8; head length 8.0; upper eyelid width 2.4; IOD 2.4; tympanum length 1.1; eye length 3.4; E-N 2.5.

Voice.—In the Macarena Mountains, Eleutherodactylus savagei began calling at dusk and choruses continued until well after midnight. The males called from low perches on leaves up to 50 cm above the ground. The call (Fig. 3) was a series of short closely spaced notes forming a dominant frequency band at 3000 Hz. Nineteen calls of 7 frogs recorded 20 March 1971 (air temperature, 17.3°C) had an average of 15 (range, 7–34) notes per call and a note repetition rate of 11.3 (10.2–12.2) notes per s. The duration of the call was 1.3 s (0.6–3.2) and the note duration was 0.05 s (0.04–0.09).

Etymology.—The new species is named for Jay M. Savage of the University of Southern California, in recognition of his contributions to understanding the biology of Neotropical *Eleutherodactylus*.

Distribution.—In addition to the type-series, we have seen the following (also from Depto. Meta, Colombia): Buenavista, 10 km NW Villavicencio, UTA 2723, 2725–26, 2741, 2743, 2748; Serrania de la Macarena, FMNH 81349–60, 81364.

Remarks.—Cochran and Goin (1970) confused this frog among what they called E. terraebolivaris Rivero (which occurs only in Venezuela). Lynch (1975) noted the presence of this frog but mistakenly termed it a member of the unistrigatus group. Eleutherodactylus savagei does not appear closely

allied to the short-legged *fitzingeri* group of frogs of the Amazon Basin (*E. lanthanites* and *E. vilarsi*). It seems to be the northwestern replacement for *E. fenestratus* (Steindachner), which is replaced in northeastern South America by *E. gutturalis* Hoogmoed, Lynch, and Lescure.

Eleutherodactylus frater (Werner)

Hylodes frater Werner, 1899, Verh. zool.-bot. Gessell. Wien, 49:479 (typelocality, Peperital, near Villavicencio, Depto. Meta, Colombia, 1000 m). Eleutherodactylus frater: Cochran and Goin, 1970, Bull. U.S. Nat. Mus. (288):433-34, pl. 54.

Diagnosis.—1) Skin of dorsum finely shagreened with scattered warts, that of venter coarsely areolate; no dorsolateral folds; 2) tympanum prominent, its length 1/4-2/5 eye length; 3) snout subacuminate in dorsal view, round in lateral profile; canthus rostralis obtuse; 4) upper eyelid as wide as IOD; no cranial crests; tubercles on upper eyelid; 5) vomerine odontophores small, low; 6) males with vocal slits, subgular vocal sac; males bearing nonspinous nuptial pads on thumbs; 7) first finger shorter than second; large pads on outer fingers; 8) fingers with narrow lateral keels; 9) 2-3 conical ulnar tubercles present; 10) small tubercles on heel; inner edge of tarsus bearing short ridge, outer edge with 2-3 conical tubercles; 11) two metatarsal tubercles, inner oval, 8 times size round outer; supernumerary plantar tubercles present; 12) toes bearing lateral keels, enlarged pads; 13) pale brown with brown markings (reverse parentheses, suprainguinal blotches, narrow limb bars, supratympanic stripe and labial bars); no canthal stripe; venter finely peppered with brown (throat darker); concealed surfaces of thighs uniform brown; 14) adults small, males 17.2–21.6 mm SVL ($\bar{x} = 20.1$, N = 7), one adult female 24.9 mm SVL.

Eleutherodactylus frater is most similar to E. incomptus Lynch and Duellman, E. marmoratus (Boulenger), and E. martiae Lynch, but differs from each in the arrangement of tarsal tubercles. It also differs from the smaller E. martiae in having vocal sacs in males and prominent tympani (concealed in E. martiae). Eleutherodactylus incomptus is probably the closest relative of E. frater but is slightly smaller (males 15.6–18.8 mm, females 23.7–25.9 mm SVL) and has the vomerine odontophores evident only in large females. Eleutherodactylus marmoratus is considerably larger (its males are larger than our only female E. frater).

Description.—Head as wide as body, wider than long; HW 35.4–38.4 (\bar{x} = 36.8, N = 7) percent SVL; snout subacuminate in dorsal view, round in lateral profile; nostrils weakly protuberant, directed dorsolaterally; snout short, E-N 69.2–87.3 (\bar{x} = 80.1, N = 7) percent eye length; canthus rostralis weakly defined, rounded; loreal region weakly concave, sloping to lips, lips not flared; upper eyelid width 93.3–113.6 (\bar{x} = 101.6, N = 7) per-

cent IOD; upper eyelid bearing 2–4 conical tubercles; no cranial crests; supratympanic fold concealing upper edge of tympanic annulus; tympanum prominent, round, its length 26.9–38.5 ($\bar{x}=33.4$, N = 7) percent eye length, separated from eye by slightly more than its diameter; postrictal tubercles subconical; choanae relatively small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores small, each $\frac{1}{3}$ – $\frac{1}{2}$ size of a choana, narrowly separated (by distance equal $\frac{2}{3}$ width of an odontophore), bearing 2–3 teeth; tongue about as long as wide, posterior border feebly indented, posterior $\frac{2}{5}$ not adherent to floor of mouth; males with relatively long vocal slits and subgular, external vocal sac.

Skin of dorsum finely shagreened, overlain with larger granulations on lower back and with larger isolated tubercles on upper eyelid, between eyes, and in scapular region; flanks becoming coarsely areolate ventrally, skin of venter areolate, that of throat smooth; no dorsolateral folds or anal sheath; discoidal folds prominent; 2–3 ulnar tubercles; palmar tubercle bifid, much larger than oval thenar tubercle (Fig. 1); supernumerary palmar tubercles smaller than more pungent, round subarticular tubercles; fingers bearing slight lateral keel, most obvious along outside of palm and finger IV; pads truncate, smallest on I, that on II intermediate, largest on III and IV (more than 2 times width of digit below pad); pad of III as large as tympanum; discs broader than long, not indented, first finger shorter than second (Fig. 1); males with white, non-spinous nuptial pad on thumb.

Small tubercle on heel, 2–3 on outer edge of tarsus, inner edge of tarsus bearing tarsal ridge (distal ½) and a tubercle proximal to ridge; inner metatarsal tubercle twice as long as wide, outer minute (less than ½ size of inner), round; supernumerary plantar tubercles small, pungent, toward distal end of sole; subarticular tubercles round, weakly pungent; toes bearing lateral keel (more fringe-like than that on fingers) and pads (about same size as on fingers but seem smaller because of toe fringe); heels of flexed hind legs barely overlap; shank 46.8-50.0 ($\bar{x}=48.9$, N=7) percent SVL.

Pale brown with slightly darker brown marbling over dorsum; still darker reverse parentheses in scapular region, slanted bars on upper flanks, and suprainguinal blotches; anal triangle dark brown; limb bars narrower than interspaces, oblique on shanks; no canthal stripe; supratympanic stripe dark brown, as are labial bars; diffuse brown area behind shoulder; ventral surfaces finely dusted with brown (most dense on throat) but appearing cream without magnification; groin peppered with brown, anterior and posterior surfaces of thighs uniform brown.

UTA 3531 has a black dorsolateral stripe continuing anteriad as a canthal stripe. There are 3 shorter brown stripes down the center of the back. Some specimens also have very pale snouts and, if so, the pale area defines an otherwise indistinct interorbital bar.

Voice.—During our 7-day camp in the cloud forest, choruses of E. frater

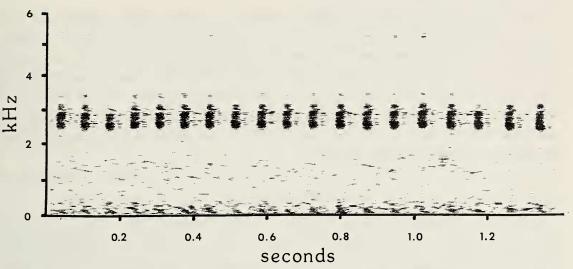


Fig. 4. Sound spectrogram of incomplete call (last 19 notes) of *Eleutherodactylus frater* (narrow band filter). Recorded 21 March 1971, Sierra de la Macarena, Colombia (air temperature, 19.7°C).

began each day at about 1500 h and continued through the evening until dark. Most individuals became quiet at dusk but a few frogs continued to call until about 1 hour after dark.

The call (Fig. 4) was a series of well-separated, short notes with a dominant frequency of about 2900 Hz. Thirteen calls of 4 individuals recorded 21 March 1971 (air temperature, 19.7°C) had a mean of 17.7 (11–32) notes per call and a note repetition rate of 16.7 (14.8–18.1) notes per s. The duration of the call was 1.1 s (0.7–2.2) and the note duration was 0.03 s (0.02–0.06).

Remarks.—Cochran and Goin (1970) confounded E. frater with the chocoan E. taeniatus (Boulenger). Lynch (1974) used the name E. frater for the chocoan species but subsequently redescribed E. taeniatus (Lynch, 1980). The eastern face of the Cordillera Oriental in Colombia is poorly known herpetologically but we anticipate E. frater and E. incomptus to replace one another somewhere between the Pasto-Mocoa road and the Bogota-Villavicencio road.

Discussion

Eleutherodactylus frater and E. savagei are similar enough in their morphology and breeding calls to make one suspect that cross matings could occur. Eleutherodactylus savagei begins calling at dusk, about 1 h before dark, so there is a 2 h interval in which the two species call at the same time. However, E. frater is almost entirely diurnal and E. savagei is essentially nocturnal, there being relatively few individuals of either species that call in the interval of temporal overlap. Furthermore, E. frater is arboreal whereas E. savagei males call from perches near the ground.

Both species produce a varying number of short notes with about the same dominant frequency, but calls of the two species can easily be distinguished by the human ear. The sound spectrograms show that the note duration of *E. savagei* averages nearly twice that of *E. frater* and that the notes of *E. savagei* are repeated at a slower rate than the notes of *E. frater*. We would expect these differences in habitat, breeding call, and time of vocalization to function as premating isolation mechanisms, making matings between the two species unlikely.

Abbreviations

Institutional abbreviations: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; KU, University of Kansas Museum of Natural History, Lawrence; USNM, National Museum of Natural History, Washington, D.C.; UTA, University of Texas at Arlington, Arlington, Texas; CM, Carnegie Museum, Pittsburgh, Pennsylvania.

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